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Environmental Suitability and Distribution of the Caucasian Rock Agama, *Paralaudakia caucasia* (Sauria: Agamidae) in Western and Central Asia

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Abstract Predictive potential distribution modeling is crucial in outlining habitat usage and establishing conservation management priorities. In this paper we provide detailed data on the distribution of the Caucasian rock agama *Paralaudakia caucasia*, and use species distribution models (MAXENT) to evaluate environmental suitability and potential distribution at a broad spatial scale. Locality data on the distribution of *P. caucasia* have been gathered over nearly its entire range by various authors from field surveys. The distribution model of *P. caucasia* showed good performance (AUC = 0.887), and predicted high suitability in regions mainly located in Tajikistan, north Pakistan, Afghanistan, southeast Turkmenistan, northeast Iran along the Elburz mountains, Transcaucasus (Azerbajan, Armenia, Georgia), northeastern Turkey and northward along the Caspian Sea coast in Daghestan, Russia. The identification of suitable areas for this species will help to assess conservation status of the species, and to set up management programs.

Keywords Western Asia, *Paralaudakia caucasia*, distribution, Maxent modeling, Agamidae

1. Introduction

Species distributions can be affected by multiple factors, such as humidity, temperature, solar radiation and elevation. Analyzing the ecological parameters affecting species distributions can help to understand underlying ecological processes, and to establish conservation strategies (Graham *et al.*, 2004). Correlative species distribution models can be extremely useful to establish conservation management priorities (Brambilla *et al.*, 2012; Jose *et al.*, 2012; Vale *et al.*, 2012a; D'Amen *et al.*, 2013). For example, such models can be used to assess the impact of global changes on species distribution (Thomas *et al.*, 2004; Fouquet *et al.*, 2010; D'Amen *et al.*, 2013), to understand biogeographic patterns (Anadon *et al.*, 2012), and to predict biodiversity (Ficetola *et al.*, 2013). Furthermore, models can identify areas where the risk of biological invasions are highest (Thuiller *et al.*, 2005; Ficetola *et al.*, 2010; Reshetnikov and Ficetola, 2011) and identify the suitable areas for threatened species. Reptiles and amphibians are ectotherms, so they often have limited climatic tolerance and are strongly dependent on climatic conditions. Therefore, bioclimatic models can be extremely useful in predicting their distribution (Buckley *et al.*, 2012).

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Recently, Baig *et al*. (2012) revised the genus *Laudakia* with the recognition of three genera: *Laudakia* Gray, 1845; *Stellagama* Baig, Wagner, Ananjeva and Böhme, 2012; and *Paralaudakia* Baig, Wagner, Ananjeva and Böhme, 2012. *Paralaudakia* is an agamid genus found in the mountain rock landscapes. Its distribution ranges from Greece and the Nile River delta on the west, through the Middle East and Central Asia, to Gobi Altai on the northeast and Brahmaputra River on the east (Ananjeva and Orlova, 1979; Ananjeva and Tuniyev, 1994; Rastegar-Pouyani and Nilson, 2002). The range of *Paralaudakia caucasia* includes the Lesser Caucasus, the Elburz Range and the Kopet-Dagh and Balkhan mountains of Turkmenistan and northeast Iran, east of the Caspian Sea (Anderson, 1999; Rastegar-Pouyani *et al*., 2007). There are also uncertain localities recorded near the Black Sea (Ananjeva and Orlova, 1979). *P. caucasia* has a fragmented distribution pattern in Iran and there are some reports of the occurrence of this species in the Zagros Mountains (Anderson, 1999). The goal of this study was two-fold. First, we gathered all available data on the distribution of *P. caucasia* to better describe its distribution range. Subsequently, we used a species distribution model to identify suitable habitat in Western and Central Asia. The results of model were then used to better understand the biogeography of the species, which may further provide important information for the conservation of the species and its habitat.

2. Material and Methods

We combined field surveys of the authors and literature records to describe the distribution of *Paralaudakia caucasia* through its entire range. Distribution data for *P. caucasia* was collected by authors from field surveys conducted in Western and Central Asia. Furthermore, we used all the available literature records (Ananjeva and Orlova, 1979; Roitberg *et al*., 2000; Anderson and Leviton, 1969; Schammakov *et al*., 1993; Tuniyev *et al*., 1998; Macey *et al*., 1998, 2000). Data from the eastern range of the species in Pakistan was collected from all possible localities in northwestern Khyber Pakhtunkhwa and north Balochistan from 1990 to 2012. The data (Appendix 1) were used to prepare a new updated distribution map for *P. caucasia*, and served as baseline to build a correlative species distribution model identifying the most suitable areas.

Maximum Entropy model (MAXENT) was used to assess the potential distribution of *P. caucasia* in Western and Central Asia (Philips *et al*., 2006; Elith *et al*., 2011). MAXENT is a machine-learning approach assessing the probability of presence in a given cell on the basis of environmental features in that cell; it is considered one of the most efficient approaches to species distribution models that does not require true absence data, and may outperform some more traditional presence/absence methods such as general linear models (Elith *et al*., 2006; Elith *et al*., 2011). Several studies demonstrated the ability of MAXENT to predict species occurrence into new geographic contexts (e.g., in other regions) (e.g., Pearson *et al*., 2007; Reshetnikov and Ficetola, 2011). MAXENT provides an index of likelihood of presence that is strongly correlated with the output of models producing the probability of presence (Li *et al*., 2011), while making a lower number of assumptions (Phillips, 2012). Additional advantages of MAXENT, compared to other software, include the possibility to integrate measures of sampling effort into models (Phillips *et al*., 2009), and its ability to establish flexible relationships between the dependent and independent variables. MAXENT is therefore well suited to evaluate complex or non-linear relationships, including thresholds, which often occur between species distribution and environmental features. The model was fitted using linear, quadratic and hinge features.

We considered six bioclimatic variables that are expected to affect physiological tolerance, metabolism and thermoregulation of reptiles, as well as water availability and productivity in ecosystems. These variables included 1) minimum temperature of the coldest month; 2) maximum temperature of the warmest month; 3) summed precipitation in the summer, the warmest season; 4) summed precipitation in the winter, the coldest season (from Worldclim; Hijmans *et al*., 2005); 5) annual solar radiation in Wh/m^2/day (Watt-hours per square meter per day) (New *et al*., 2002); and 6) Normalized Difference Vegetation Index, which is a measure of primary productivity (Gutman *et al*., 1997). We did not include altitude because it is strongly collinear to temperature (Harris *et al*., 2013). All variables were at the resolution of 10 × 10 arc primes. In the model, we used accessibility (Nelson, 2008; Uchida and Nelson, 2010) as a measure of sampling bias, assuming that sampling may be easiest in the most accessible regions (Phillips *et al*., 2009; Ficetola *et al*., 2013). MAXENT provides an index of likelihood of presence; in our analysis, we used a logistic output, with MAXENT suitability ranging from zero (no suitability) to one (maximum suitability).

We used cross-validation to assess the predictive performance of the model. Data were split in ten sets.

We built a model using 90% of the data (calibration data) and tested predictive performance for the remaining 10% of the data (test data). This procedure was repeated ten times, each time using a different set of test data (Nogués-Bravo, 2009). As a measure of model performance, we calculated the area under the curve of the receiver operator plot (AUC) for the test data and averaged over the ten replicated runs as a measure of predictive performance. Models with AUC = 0.5 indicate a performance equivalent to random; AUC > 0.7 indicates useful performance, AUC > 0.8 indicates good performance and AUC ≥ 0.9 indicates excellent performance (Manel *et al.*, 2001). Next, we used a Z test comparing observed frequencies of correct and incorrect predictions to evaluate if the model predicts distribution significantly better than expected under random expectations. For this test, we assumed that a cell is suitable if its suitability was larger than the maximum test sensitivity plus specificity threshold (Gallien *et al*., 2012). To evaluate the relative importance of environmental variables, in each iteration of the algorithm, the increase in regularized gain was added to the contribution of the corresponding variable, or subtracted from it if the change to the absolute value of lambda was negative. Relative importance of variables was calculated as the average over the ten replicated runs. The suitability map was calculated using the logistic output of MAXENT as the average suitability across the ten runs of cross-validation; in the output map we considered that a cell is suitable if its suitability was larger than the maximum test sensitivity plus specificity threshold (Gallien *et al*., 2012).

3. Results

We obtained records of *Paralaudakia caucasia* from 167 localities in Western and Central Asia (Figure 1, Appendix 1). The distribution of *P. caucasia* includes the region in the eastern half of the Caucasus, north-eastern Turkey, in northern Iran, Iraq, Afghanistan, north-western Pakistan and in the south of Middle Asia. Further to the east there are records from the vicinity of Chubeck (southern Tajikistan). On the territory of Russia the species occurs in Daghestan, in the vicinity of the settlement Kumtor-Kala and near the settlements Akhty and Rutul.

The MAXENT model described the distribution data well, as the average AUC for test data was 0.887, indicating good performance. The value of 0.27 was the suitability threshold optimizing the model predictions. The model consistently predicted suitability in test data much better than expected by chance ($P < 0.0001$ in all replicated runs), confirming the good performance of the model. Winter precipitation and annual maximum temperature were the variables with the highest contribution to the model, as they showed the highest average percent contribution over the ten replicated models (Table 1).

The model indicated that the northern belt of Iran, eastern Turkey, Armenia, Georgia, Russia, Tajikistan and Himalayan Mountains are the most suitable regions for *P. caucasia*. According to the predictive map, most regions in the southern mountains of Iran and the area between Iran-Afghanistan are unsuitable for *P. caucasia* (Figure 1).

Table 1 Relative importance of variables included in the best model. To evaluate the relative importance, in each iteration of the algorithm, the increase in regularized gain was added to the contribution of the corresponding variable, or subtracted from it if the change to the absolute value of lambda was negative. Relative importance was calculated as the average over the ten replicated runs.

Variables	Percent contribution
Winter precipitation	34.6
Maximum temperature	20.9
Summer precipitation	18.2
Solar radiation	11.7
Minimum temperature	9.6
NDVI	5

4. Discussion

The results confirm the known distribution of *Paralaudakia caucasia*. According to the model, suitability is highest in Elburz Mountains, Kopet Dagh and Caucasus region, which are also the areas where most of known populations of the species are present (Macey *et al.*,1998, 2000). However, most of the southern mountains of Iran and the area between Iran-Afghanistan seem to be unsuitable for *P. caucasia*. The model map confirms the supposed isolation of the populations of this species in Daghestan, Russia and within Azerbaijan in the Apsheron peninsula and in Gobustan (Ananjeva and Orlova, 1979) (Figure 1). Other Trans-caucasian populations are within a large cluster and can be considered as a major area of environmental suitability of *P. caucasia*. There is one additional cluster in Elburz with an independent cluster eastwards of the Caspian Sea. The map does not show isolated Balkhan populations and population of Krasnodoskoye plateau.

The model identified potentially suitable regions outside the known range of *P. caucasia*. For instance,

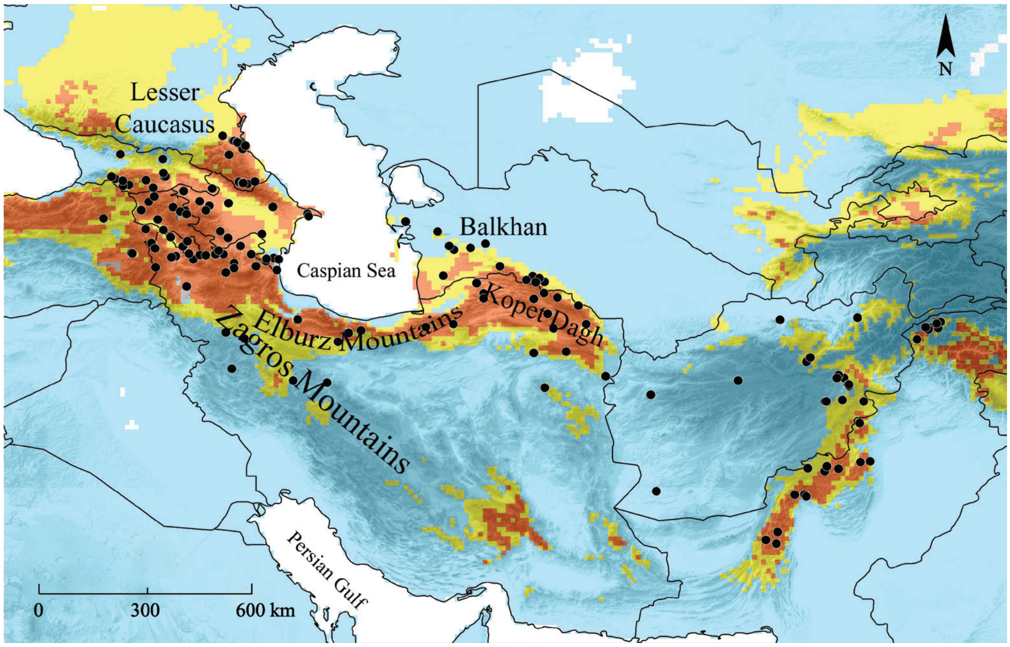

Figure 1 Potential distribution modeling of *Paralaudakia caucasia* in Central and Western Asia. Colors in the map indicate different suitability values: Blue: suitability < 0.27; Yellow: 0.27 ≤ suitability < 0.5; and Orange: suitability > 0.5. The maximum test sensitivity plus specificity threshold is 0.27, and it indicates suitability for the species (Gallien *et al*., 2012); values > 0.5 indicate very high suitability, as 0.5 is the typical MaxEnt suitability of presence points used for calibration (Elith *et al*., 2011).

suitable areas are identified in Kerman Province, Iran and south of the Black Sea in Turkey, where the species is absent. This may be due to dispersal limitation or biotic interactions, such as interactions with related species (e.g., *P. microlepis*, *Laudakia nupta*, *Stellagama stellio*) (Anderson, 1999; Sindaco and Jeremčenko, 2008). Furthermore, our analysis has been performed at a broad spatial scale, covering the whole range of the species, and therefore has focused mostly on abiotic variables. Nevertheless, at a local scale, variables representing substrate, vegetation and habitat availability may be more important (Dezphoulian *et al*., 2012).

P. caucasia has a significant intraspecific genetic structure. Macey *et al*. (2000) identified three major groups: western populations in the Caucasus, central populations in Elburz and Eastern populations in Balkhan and Kopet-Dagh. No genetic data is currently available for the easternmost populations from Afganistan and Pakistan. Macey *et al.* (2000) proposed that tectonic processes are at the basis of differentiation among populations. Tectonic processes first fragmented populations in Lesser Caucasus and Elburz Mountains from those in the central and eastern part of the range (Elburz + Balkhan/Kopet-Dagh) about 2–3 MYA, while a more recent split (about 2.1 MYA) occurred between the Elburz populations and the eastern populations (vicariance hypothesis; Macey *et al*., 2000). Nevertheless, the distribution model suggests the existence of a strip of continuous suitable habitat between Caucasus, Elburz, and populations east to the Caspian Sea (Figure 1), suggesting potential contact between these populations. On the other hand, the easternmost populations from Afghanistan and Pakistan seem to be isolated from the other populations (Figure 1). Studies are needed to analyze the genetic makeup of these populations. Detailed taxonomic and genetic studies would also be valuable for partially isolated populations, such as those in isolated Daghestan, Apsheron.

A comparison of the distribution of *P. caucasia* with their closely related species *P. microlepis* is needed to better understand factors that determine each species distribution (e.g., competition versus differences of ecological niche), and to assess the relative importance of biogeographical and ecological processes that differentiate these species. Furthermore, species distribution models are a key step for conservation plans of poorly known species, as they allow to estimate their potential geographic distribution and the environmental factors (e.g., climate) that allow the abiotic conditions suitable for a species presence. In absence of more refined data, these maps may provide useful information to identify suitable areas that help to assess conservation status and to set up management programs at broad geographic scale for target species or communities (Corbalan *et al*., 2011;

Vale *et al.*, 2012b; Lyet *et al.*, 2013). The results of this study are a key starting point for a better understanding of the ecological requirements of *P. caucasia*, and can be integrated with fine scale data on habitat and threats, or with data on additional species, to build appropriate strategies for management and conservation.

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Appendix 1 All coordinate data for *Paralaudakia caucasia* for its entire distribution used in this study.

Number	Latitude	Longitude	Number	Latitude	Longitude	Number	Latitude	Longitude	Number	Latitude	Longitude
1	36.58	66.83	2	35.08	67.78	3	33.67	68.45	4	33.67	68.50
5	34.42	65.33	6	33.90	62.20	7	34.60	68.93	8	34.50	69.13
9	31.52	70.07	10	33.72	69.07	11	33.67	69.83	12	34.60	68.93
13	36.67	69.62	14	34.50	68.88	15	40.50	45.50	16	39.67	48.25
17	36.13	51.35	18	38.83	45.00	19	38.93	47.87	20	38.37	48.78
21	36.43	55.12	22	37.53	56.20	23	30.45	62.40	24	28.70	66.33
25	42.97	47.50	26	40.22	42.57	27	39.83	44.08	28	38.98	43.57
29	38.97	43.60	30	38.02	58.03	31	38.50	56.78	32	37.95	58.38
33	38.15	57.97	34	38.08	58.20	35	38.02	57.73	36	37.93	58.07
37	38.17	54.75	38	40.10	53.40	39	39.75	54.55	40	39.17	55.73
41	39.10	55.13	42	39.23	54.97	43	39.32	56.27	44	39.23	47.48
45	34.42	49.37	46	38.87	45.17	47	36.12	51.32	48	36.80	58.50
49	36.20	51.80	50	35.80	50.98	51	41.70	44.75	52	37.78	45.55
53	38.93	46.87	54	38.80	48.67	55	37.33	58.00	56	37.55	58.37
57	37.10	59.60	58	34.57	60.58	59	35.40	58.00	60	34.15	58.40
61	36.28	58.72	62	37.90	55.95	63	36.33	54.13	64	38.62	47.25
65	38.75	45.78	66	37.38	58.85	67	34.33	50.58	68	35.92	47.62
69	36.13	46.95	70	38.43	47.25	71	38.28	46.95	72	38.50	48.03

(Continued Appendix 1)

Number	Latitude	Longitude	Number	Latitude	Longitude	Number	Latitude	Longitude	Number	Latitude	Longitude
73	38.93	46.58	74	39.33	44.28	75	39.15	44.42	76	38.87	45.17
77	38.83	45.00	78	36.43	59.88	79	36.80	58.50	80	35.45	59.17
81	37.35	56.20	82	36.12	51.37	83	34.83	47.17	84	38.47	44.43
85	36.60	49.53	86	39.23	47.48	87	43.18	46.84	88	43.00	47.21
89	43.00	47.25	90	42.97	47.35	91	42.87	47.46	92	42.92	47.46
93	42.71	47.56	94	42.50	47.07	95	41.54	47.43	96	41.50	47.56
97	41.46	47.73	98	42.94	47.37	99	41.55	48.00	100	41.49	47.57
101	42.82	47.66	102	40.40	49.88	103	40.29	49.92	104	40.68	46.36
105	40.51	46.24	106	40.63	48.64	107	39.07	46.70	108	39.52	47.03
109	39.76	46.75	110	38.91	46.03	111	39.21	45.41	112	39.55	44.97
113	39.41	45.57	114	38.69	48.39	115	38.78	48.42	116	38.75	48.85
117	38.96	45.63	118	38.90	46.23	119	41.73	44.79	120	41.29	46.46
121	41.84	44.72	122	42.52	43.17	123	41.64	42.98	124	41.71	42.85
125	41.41	43.48	126	41.59	44.09	127	41.38	43.26	128	41.32	44.35
129	42.35	44.69	130	41.57	43.26	131	40.18	44.51	132	40.52	43.92
133	40.81	44.19	134	41.01	44.39	135	39.81	44.71	136	40.62	45.05
137	40.47	45.32	138	40.37	45.55	139	41.19	45.44	140	40.77	47.05
141	40.83	46.02	142	28.57	66.70	143	28.99	66.75	144	30.32	67.37
145	30.32	67.73	146	30.33	67.71	147	30.26	67.77	148	31.25	68.94
149	31.27	67.83	150	31.17	68.43	151	31.34	68.52	152	31.49	69.72
153	32.89	69.70	154	34.21	69.29	155	34.21	69.30	156	34.26	69.27
157	34.21	69.31	158	34.27	69.31	159	35.89	71.76	160	35.89	71.76
161	35.24	67.92	162	36.31	72.22	163	36.25	72.15	164	36.30	72.51
165	36.52	72.60	166	36.45	72.46	167	36.31	72.06			